

Opinion.

Reply to Scott's Criticism

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Differences of interpretation amongst authors dealing with the same set of facts are only to be expected in the literature of phylogenetics. However, when an author's work receives heavy refutation on grounds which (a) grossly misrepresent his own viewpoint, and (b) lean heavily on wrongful statements *of fact*, then it is necessary and right that these misrepresentations be exposed. The paper by Scott (1986) in this journal is the subject of the following commentary.

The following notes on the distribution of character states of Ditrysian Lepidoptera show that Scott's factual evidence runs contrary to established knowledge.:

Larval Characters:

(1) The loss of L3 on the prothorax is not restricted to Pyraloidea and 'Macrolepidoptera' — it is also found in the Scardiinae (Tineidae), Zygaenoidea, Epermeniidae and Glyphipterigidae-*sensu* Brock. Scott gives no explanatory comment on his placing of Carposinidae in Pyraloidea — and his placing of Mimallonidae in that superfamily runs contrary to characteristics of adult and pupa, his observations on larval morphology having been known since the work of Fracker (1915). In addition, some Pyraloidea (*sensu* Scott) actually *possess* the 'missing' L seta (Forbes, 1923). (2) Scott offers no reason for assuming that the Pyraloid 'L' group is *primitively* unisetose on abdominal segment nine. It is *often* bi- (sometimes tri-) setose in that superfamily. Again, the supposed absence of two of the three 'L' setae on the same segment for 'Macrolepidoptera' is in opposition to the presence of two 'L' setae on segment nine in Notodontidae and Drepanidae (Hassenfuss, 1969). The same reduction trend is seen in many members of the Tineoid complex (MacKay, 1972). (3) Scott is correct in stating that all 'Macros' have L1 and L2 separate on the abdomen. However, these setae are also dissociated in the (extralimital) Immidae (Common, 1979), and in monotrysian Heteroneura, Tineoidea *s. str.* (excluding Psychidae) and

Yponomeutoidea *sensu* Brock. Other correlations of chaetotaxy could be taken to show that the 'Macros' evolved from Cossoidea. The condition of the 'L' setae in Mimallonidae (see above) could equally well serve as evidence that these setae were associated in the 'Macro' ancestor — as indeed suggested by Forbes. These 'wide-gap' character states occur separately in different families of Tineoidea *sensu stricto*. (4) The presence of secondary setae cannot be taken as a shared-derived trait of 'Bombycoidea-Sphingoidea-Hesperioidea-Papilionoidea'. Similar secondary vestiture is found in the (extralimital) Zygaenidae — and it is certainly *not* 'absent in Noctuoidea' as claimed by Scott (cf. Arctiidae, Ctenuchidae, Notodontidae, Acronictinae, etc.). (5) Reduction of crochets from circlet to mesoseries is found within many ditrysian superfamilies, and the 'butterfly triserial condition' is found in some Cossoidea and Pyraloidea — even in groups as remote as Gelechioidea (Forbes, 1923). Intermediate stages are found in Geometroidea, as well as in Rhopalocera (amongst 'Macrolepidoptera').

Pupal Characters:

All characters of the 'Macrolepidopterous' pupa are found also in the 'Micro' groups Yponomeutoidea and Gelechioidea — while Scott's ancestor for Pyraloidea-Macrolepidoptera is clearly an incompletely obtect pupa. 'Spinose-protruded' pupae also occur in some Bombycoidea and Forbes (1923) records pupal protrusion for certain Pyraloidea. Some Psychidae have 'incomplete' male pupae, and obtect females!

Looking in greater detail at Scott's listing of pupal characters, it must be stated that: (1) Maxillary palpi are not 'lost' in 'Macros' — as stated by Mosher (1916) they are developed externally in many Noctuidae. (2) In placing Sphingidae in his Hesperioide-Papilionoid lineage, Scott cites 'loss of cocoon' as a shared derived trait — yet some Sphingidae are cocoon-builders. (3) Contrary to Scott's claim, neither Zygaenoidea nor Sesiioidea have two rows of spines per segment. The primitive condition is one row for Zygaenidae, the spination becoming more diffuse in advanced forms. In Sesiioidea, there is a single row per segment in Choreutidae — double rows only in Sesiidae and Brachodidae (Heppner and Duckworth, 1981). Similarly, the Tineoid superfamilies do not 'generally have one row...'; in this group, the Yponomeutoidea and Gelechioidea are never spinose/protruded — excluding genera of Tortricoid-Sesioid-Zygaenoid relationships wrongly placed in Yponomeutoidea by Common (1970) — see Brock, (1967, 1971), Heppner and Duckworth (*loc. cit.* above), Heppner (1977) and Kyrki (1984). Lyone-tiid pupae are also non-spinose, and *two* spine rows have apparently evolved independently in some members of the families Psychidae and Gracillariidae (Mosher, 1916). (4) Mandible remnants are *not* 'definite bumps in Cossoidea-Castnioidea, weakly developed in butterflies'; the 'Cossoid-Castnioid condition' is widespread amongst 'moths' and the (non-

unique) 'butterfly condition', far from being weakly developed, involves an *enlargement* of these structures — so that right and left 'mandible remnants' almost meet along the median line (Mosher, 1916). In the same way, development of the clypeo-labral suture is variable in Ditrysia, and cannot be used as a 'shared-derived trait'. (5) Having used the presence of fore leg femur in the pupae of 'nearly all moths' (cf: 'shared-derived traits for monophyly of Hesperioidea-Papilionoidea'), Scott goes on to list the *exclusive* presence of the same trait as evidence for primitiveness of Geometroidea and Noctuoidea within his Macrolepidoptera. Loss of a visible fore-leg femur is also quite widespread amongst Microlepidoptera (Mosher, 1916). (6) Scott uses the presence of an epicranial suture/cleavage line as a further indicator of the primitive position of Geometroidea-Noctuoidea within 'Macros', yet fails to state the presence of this trait in some Bombycoidea; his substitution of *temporal* for 'epicranial' is based on an unlikely pupal-imaginal homology (Scott, 1985), and his statement (*loc. cit.*, and in the present diatribe) that the epicranial cleavage line is absent in Lycaenidae (contrary to Mosher) is incorrect.

Adult Characters:

(1) Vestigation of the Cup vein in the forewing is widespread amongst lower ditrysians (including some Cossoidea-Zygaenoidea), and in any case this vein is well developed in certain Bombycoidea. It cannot therefore be a 'shared-derived trait' of Macrolepidoptera. (2) Sharplin's summary of character states associated with the wing base in Lepidoptera (Sharplin, 1964) clearly states that Cossoidea, Castnioidea and Zygaenoidea either exhibit intermediate conditions between primitive and advanced Ditrysia, or else they carry advanced ('Macro') character states. Scott's manipulation of the Sharplin data requires support from described morphological observations — together with some indication as to how Sharplin herself came to be misled. (3) The 'discrimen' (mesal lamella) of the mesothorax shows variable development in Ditrysia, and its strengthening in 'Macros' is not an exclusive (or universal) attribute of these superfamilies (Brock, 1971). (4) The looped heart of 'Macrolepidoptera' is also developed in many Cossidae and Limacodidae — although not in Pyraloidea. Scott also states that 'moths' other than some Cossidae 'lack a chambered heart', following Hessel (1969), while the latter author states quite clearly (*loc. cit.*) that most 'Macro-moths' *do* have a chambered heart. Hessel's distinction between the groups cited by Scott was not dependent upon *presence/absence* of the heart chamber — but on *transverse versus horizontal orientation of the chamber itself*. (5) Scott presents no evidence whatsoever for his assertion that the Bombycoidea-Sphingoidea evolved from a tympanum-bearing ancestor. According to his scheme, the abdominal tympanum of Pyraloidea was ancestral to that of Geometroidea and Noctuoidea — yet

many Pyraloidea and Geometroidea lack a tympanum, and there is no definite evidence that this is a secondary development in either case. There is also evidence to suggest that the Noctuid tympanum evolved *in situ* (i.e., on the thorax), rather than being a later advance on an originally abdominal tympanum. (6) The presence/absence of ocelli, chaetosemata and haustellum in Ditrysia follows such a widespread pattern of correlation in the taxonomic hierarchy, that no importance can be attached to this, above the level of family (Brock, 1971). (7) The loss of the upper sector of the precoxal suture/sulcus cannot be brought forward as a shared-derived trait for Bombycoidea-Sphingoidea-Rhopalocera. As stated by Brock (1971), this trend is widespread in other ditrysiian superfamilies in which the suture is sometimes retained. Scott's treatment of this suture also implies two misidentifications in Brock (*loc. cit.*) — firstly, in his use of quotation marks: 'precoxal suture' of Brock; in fact, the term *paracoxal* is nothing more than a doubtfully necessary replacement term of Matsuda (1970) for the widely used *precoxal*. Secondly, Scott states (here, and in Scott, 1985) that the structure identified as 'precoxal suture' by me for HesperIIDae, is in fact the secondary sternopleural suture (a term originated by me to replace a misnamed suture of Ehrlich, 1958, still misapplied by Kristensen, 1976). If a secondary sternopleural suture does occur in HesperIIDae other than those I examined, then (a) Scott must name and figure examples, and (b) we require a more acceptable explanation from Scott as to why the precoxal suture vestige figured by me is 'misidentified'. (8) The distal enlargement of the antenna reported by Scott for Sphingidae (as a shared derived trait with Rhopalocera) is absent in many Sphingids (and present in many diurnal moths — e.g.: Agaristinae, Castniidae, Zygaenidae, Callidulidae, etc.). Its presence is clearly correlated with diurnal activity. (9) The 'areole' of the forewing radial system does not 'occur in most moths' — it is limited to a few families of Noctuoidea and Geometroidea and one of Bombycoidea, amongst 'Macros'. It is unlikely that true homology exists between the 'areoles' of these groups, or between any one of them and the (similarly sparsely distributed) 'areole' of lower Ditrysia (Brock, 1971). (10) The R4/5 branching basad of R1 in the radial system of Rhopaloceran pupae is found also in adult Castniidae (see Forbes, 1923). Published sources of data on pupal tracheation of 'moth' groups are too fragmentary to allow broad generalisations to be made at this stage. (11) Fusion of the anapleural cleft, listed as a shared-derived trait for Hesperioidea-Papilionoidea by Scott (contrary to Kristensen, 1976 — following Brock, 1971) is a feature of some diurnal 'moths' (and in any case, is not apparent in HesperIIDae). (12) 'Mesal fusion of the metathoracic furcal arms' is also listed as a shared derived trait of Hesperioidea-Papilionoidea by Scott, but this occurs also in Pyralidae (although not in other Pyraloidea — see Brock, 1971). Scott also erroneously refers to fusion of furcal *arms* — whereas it is the *dorsal laminae* of these structures which form the fusion (this same

character is listed by Kristensen, 1976 as a 'probable synapomorphy' of the same group). (13) The reduction of sternal apodemes (of abdominal sternite two) in Rhopalocera is a widespread trait in Ditrysia — including Limacodidae, Saturniidae, Thyrididae, and of course, many tympanum-bearing families (Brock, 1971). (14) Scott mentions similarities between Hesperiiidae and 'Macro-moths' in compound eye structure. Following Yagi and Koyama (1963), this correlation lies with the more primitive Bombycoidea *alone* — although these workers report a similar correlation with the 'non-Macro' *Cossidae* — a fact not mentioned by Scott. The same authors found a natural lineage between the compound eye conditions of Pyraloidea-Geometroidea-Noctuoidea, this apparently unconnected with the Cossoid/Hesperioid/lower Bombycoid eye — although many convergencies were evident between diurnally active members of quite remote families. These broader findings are entirely ignored by Scott. In the lack of any good functional explanation of the data on the compound eye, we do not know how (or *if*) the Cossid condition could form a transition to that of the supposed Pyraloid lineage — although its (theoretical) connections with Hesperioidea and Bombycoidea are clear enough. (15) Scott lists the reduced condition of the maxillary palpi in 'Macrolepidoptera' as diagnostic, yet three-segmented palpi are reported for Carthaeidae of Bombycoidea by Common (1966, cited in Brock, 1971). Reduction of palpi is found in many 'Microlepidoptera', including Cossioidea, Zygaenoidea, and even Tineoidea (Psychidae).

Given the high degree of polyphyly in the characters listed, it is not possible to use them either as diagnostic features of suprafamilial groups — or as monophyletic character changes along the branches of Scott's phyletic tree. Many provide useful suprageneric characters, but all are known to be unstable at higher levels. Scott also uses *primitive* character states as indicators of affinity (as indeed in his parallel paper on butterfly phylogeny, Scott 1985). This 'phenetic' approach is universally rejected by all cladists. In the same way, Scott's use of 'secondary loss' characters cannot have much relevance to phylogeny reconstruction.

Scott's attack on certain phyletic relationships suggested by me completely overlooks the *indirect ancestor concept* (see Cracraft, 1974), yet this too is regarded as a fundamental principle by phylogenetic systematists. *No* direct ancestor relationship was ever proposed by me, for any ditryisian superfamily pair — and to argue against theories of *indirect* relationship on these grounds is nothing more than the knocking-down of a 'straw man' hypothesis.

Scott's table of characters actually shows 'plus-minus' entries (providing 'modified weighting') for some characters listed in the accompanying text as either 'plus' or 'minus' for the same taxa. An expansion of this table to incorporate all other characters (and all other Ditryisian superfamilies — with many more 'pluses' and 'minuses' corrected to

'plus-minus') would agree pretty well with the general conclusions of Brock (1971) regarding the lability of the vast majority of characters available for higher classification and phylogeny reconstruction at superfamily level and above in Ditrysia.

Looking more deeply into the question of misrepresentation of my own views — I find no mention whatsoever of the fact that my 'selection of characters' was empirically based (*loc. cit.*, p. 30). My final analysis was stated, character-by-character, at some length — far from being the 'intuitive' system Scott claims it to have been. That analysis was placed firmly in perspective with the broadest conclusions of the classical authors working with the early stages, with actual quotations from the contributions of Hinton (1952) and Chapman (1896) incorporated in the text. In the same way, the broader conclusions of Yagi and Koyama (1963) and of Hessel (1969) are either ignored or misrepresented by Scott.

Based on the widespread manifestation of polyphyletic trends at and above superfamily level in Ditrysia, I had argued that an explanation could be found in the phenomenon of gradistic evolution (following the terminology of Huxley; cf. Huxley, 1942/63) — and that the higher groups Macrolepidoptera and Microlepidoptera were in fact, gradistic constructs — this hypothesis being based on three main facts: (1) the diagnostic traits of 'Macro' grade had virtually all evolved in several 'Micro' superfamilies, (2) the majority of 'Micro' grade characters are to be seen distributed amongst primitive members of the 'Macro' superfamilies, and (3) most of these trend characters seemed correlated with the change-over from endophagous to exophagous larval habits. This is not the place to go into this hypothesis in detail, but Scott omits all reference to this central theme of my earlier paper. Subsidiary to that thesis, was an arguable hypothesis for cladistic relationships between members of 'Macro' and 'Micro' grade, based upon those trends which seemed the least labile. The gradistic concept of large-scale evolutionary change presents an obstacle to those cladists who are certain that phylogeny can always be worked out on the basis of 'synapomorphy' and gradism has the further 'wrong' attribute of being highly 'non-parsimonious'. Whichever way we look at the data for Ditrysia, there are virtually *no* 'synapomorphies' for units above superfamily — with many superfamilies themselves based on polythetic distribution of character states for included families. Basic to the question of gradistic evolution is the related typological problem of 'wide phenetic gaps' between 'Micro' and 'Macro' superfamilies. For example, arguments concerning the possibility of an indirect ancestry relationship between Castnioidea and Rhopalocera invariably cite 'Micro' grade features of Castnioidea (many of them lost in advanced Castniids!) as evidence of 'unbridgeable gaps' between these taxa. The strongest of these 'gap' character complexes lie with the larval and pupal stages — yet no one objects to similar 'gaps' existing within families which display both

endo- and exophagous biology (e.g., Pterophoridae, see Brock, 1971). Secondly, the same authors seem unconcerned by the presence of 'incomplete' and obtect pupae within single families like Yponomeutidae (*sensu* Common) and the Lyonetiidae of many recent authors. Either these features are indicative of 'unbridgeable gaps' (equals Special Creation?) or else they are potentially rapid adaptations (as suggested by their taxonomic correlations).

The exceedingly widespread expression of parallelism at higher levels in Ditrysia surely points to a major feature of the evolutionary process itself, rather than an attempt by Brock to upset the theories of some cladists and pheneticists. The way forward from this point must surely be to look more deeply into the morphology of the lower Ditrysia, and to re-examine larval and pupal morphology — looking for functional explanations in these data — along with that presented by Yagi and Koyama on the compound eye and by Hessel on the aorta and associated structures. Anything less stands in grave danger of being categorised as what H.E. Hinton once described as 'a kind of juggling with the facts — by persons with limited direct knowledge of the facts'. Granted, there are alternative theories to the one I proposed — but we require better representation both of existing knowledge *and* of other proposed theories, than that now put forward by Scott. Impediments to such progress are numerous — many families of Ditrysia are poorly represented in collections and often early stages are little known — even undiscovered. Functional explanations of morphological trends are often evasive. Some authorities in a position to help with certain of these problems are actually hostile to the continuation of work of this kind — many lepidopterists will only support work in 'safe areas' which pose no apparent threat to established classifications — 'the stability of Lepidoptera classifications since Herrich-Schaeffer' having been one 'justification' for a personal attack on my work by an 'authority' at the British Museum in London, which probably did more than anything to impede further progress.

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